

REPORT DOCUMENTATION PAGE			Form Approved OMB NO. 0704-0188		
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1. REPORT DATE (DD-MM-YYYY) 10-05-2017		2. REPORT TYPE Final Report		3. DATES COVERED (From - To) 1-Sep-2013 - 31-Aug-2016	
4. TITLE AND SUBTITLE Final Report: Dynamics at intermediate time scales and management of ecological populations (Research Area 3: Mathematics)			5a. CONTRACT NUMBER W911NF-13-1-0305		
			5b. GRANT NUMBER		
			5c. PROGRAM ELEMENT NUMBER 611102		
6. AUTHORS Alan Hastings			5d. PROJECT NUMBER		
			5e. TASK NUMBER		
			5f. WORK UNIT NUMBER		
7. PERFORMING ORGANIZATION NAMES AND ADDRESSES University of California - Davis Sponsored Programs 1850 Research Park Drive, Suite 300 Davis, CA 95618 -6153			8. PERFORMING ORGANIZATION REPORT NUMBER		
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS (ES) U.S. Army Research Office P.O. Box 12211 Research Triangle Park, NC 27709-2211			10. SPONSOR/MONITOR'S ACRONYM(S) ARO		
			11. SPONSOR/MONITOR'S REPORT NUMBER(S) 63865-MA.8		
12. DISTRIBUTION AVAILABILITY STATEMENT Approved for Public Release; Distribution Unlimited					
13. SUPPLEMENTARY NOTES The views, opinions and/or findings contained in this report are those of the author(s) and should not be construed as an official Department of the Army position, policy or decision, unless so designated by other documentation.					
14. ABSTRACT Progress supported by this proposal ranged from basic mathematical advances to applications of these advances to issues in ecology and management of ecological systems. One of the most basic approaches for understanding transient dynamics is based on non-autonomous differential equations, which were used to look at the transit time and residency time of particles in compartmental systems, with potential application to understanding the dynamics of carbon pools. Studying transient dynamics of structured populations led to problems of understanding spectral bounds of matrices which allowed an understanding of interplay between time scale of response of populations and					
15. SUBJECT TERMS Differential equations, timescales, ecology					
16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT UU	15. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON Alan Hastings
a. REPORT UU	b. ABSTRACT UU	c. THIS PAGE UU			19b. TELEPHONE NUMBER 530-752-8116

RPPR
as of 25-Aug-2017

Agency Code:

Proposal Number:

Agreement Number:

Organization:

Address: , ,

Country:

DUNS Number:

EIN:

Date Received:

Report Date:

for Period Beginning and Ending

Title:

Begin Performance Period:

End Performance Period:

Report Term: -

Submitted By:

Email:

Phone:

Distribution Statement: -

STEM Degrees:

STEM Participants:

Major Goals:

Accomplishments:

Training Opportunities:

Results Dissemination:

Plans Next Period:

Honors and Awards:

Protocol Activity Status:

Technology Transfer:

1 Problem Studied

Despite many advances in developing alternative approaches, the majority of theoretical approaches to ecological questions still have been based on the asymptotic analysis of deterministic models with constant parameters. Notable exceptions include the use of stochastic approaches, but in these cases the primary tools have been models with small noise that is uncorrelated through time. Yet, in ecology, major questions depend on dynamics on intermediate time scales where asymptotic behavior would not be an appropriate assumption. And, changes in environmental conditions over time indicate that it is important to include temporal changes in any models.

Progress supported by this proposal ranged from basic mathematical advances to applications of these advances to issues in ecology and management of ecological systems. One of the most basic approaches for understanding transient dynamics is based on non-autonomous differential equations, which were used to look at the transit time and residency time of particles in compartmental systems, with potential application to understanding the dynamics of carbon pools. Studying transient dynamics of structured populations led to problems of understanding spectral bounds of matrices which allowed an understanding of interplay between time scale of response of populations and time varying environments, which would also have broad applicability beyond population biology. Ideas like this were extended to understanding the role of autocorrelation through time on linear dynamics over relatively short time scales, which was then used to understand invasive species dynamics. These more basic ideas were also then applied to understanding spatial responses of individuals, and to management of eutrophication in lakes. The overall ideas and importance of time scales as a unifying principle to guide management of ecological systems were then summarized as part of a Sackler colloquium held at the National Academy of Sciences. Progress in a number of areas has been achieved and here I will briefly summarize the work in the papers (listed in the bibliography at the end) and provide more details on other approaches.

2 Dynamics of simple food web modules

We (the postdoc on the project, Gabriel Gellner and I, together with another collaborator, Kevin McCann) made substantial progress in the analysis of solving simple two and three species differential equation models of ecological systems, as described in the proposal and in a paper focusing on the two species case published in 2016. The underlying ideas are relatively simple, essentially depending on the idea that previous failures to understand non-monotonic dependence of stability on parameter changes come from not recognizing changes in eigenvalues from real to complex as parameters are varied. Coupling this idea with stochastic simulations of dynamics yields new insights into the impact of variability on stability of ecological systems, and on appropriate definitions of stability. We argue using the classical type II consumer-resource model as an

example where the frequently used empirical metric, CV, hides two different, but important aspects of stability: (i) stability due to mean population density processes, and; (ii) stability due to population density variance processes. We then employ a simple stochastic consumer-resource framework in order to elucidate: (i) when we expect these two different processes to arise in ecological systems, and importantly; (ii) highlight the fact that these two stability processes respond differentially, but predictably, to changes in fundamental parameters that govern biomass flux and loss in any Consumer-Resource interaction (e.g., attack rates, carrying capacity, mortality). Further work is ongoing to look at extending these ideas to more complex systems.

3 Equation free modeling and temporal scales

A graduate student partially supported by the grant, Noam Ross, and I have been looking at analyses of systems based on the approach of equation free modeling due to Kevriekedes, which essentially is a way of explicitly recognizing the different time scales inherent in the problem. The approach has been applied to a system modeling the dynamics of a fungal disease of trees with the goal of understanding what the best control measures would be. The results can be compared to an optimal control approach of a mean field model. The ideas clearly would have broad applicability to other diseases, as well as to other spatial control problems that would be essentially impossible to approach by other means. This work has yet to be published.

4 Nonautonomous differential equations

Transient dynamics often reflect exogenous variability in the system under study. In fact, in ecological systems, the importance of transient behavior, as opposed to asymptotic behavior, is often a reflection of the fact that the ecological system is in a perpetual transient in response to external forcing. Under this project, several approaches are being used to analyze this and are covered in the last headings in this report. One approach is to use ideas from the theory and analysis of non-autonomous differential equations, as recently summarized by Klode and Rasmussen. For these systems even definitions of stability and other ideas are changed. The challenge is to develop approaches that lead to computationally tractable methods. With Rasmussen and others, we have been applying these ideas to understanding the dynamics of linear compartmental models, as would arise for example in models of carbon cycling, to understand dynamics as external changes occur, e.g. global change. A summary of the problem (and results) from a mathematical point of view follows.

A (linear) *autonomous compartmental system* with d pools is given by an inhomogeneous linear differential equation

$$\dot{x} = Bx + s, \tag{1}$$

where $B \in \mathbb{R}^{d \times d}$ is an invertible matrix, $0 \neq s \in [0, \infty)^d$, and the entries $\{b_{ij}\}_{i,j \in \{1, \dots, d\}}$ of the matrix B satisfy

- $b_{ii} < 0$ for all $i \in \{1, \dots, d\}$,
- $b_{ij} \geq 0$ for all $i \neq j \in \{1, \dots, d\}$,
- $\sum_{i=1}^d b_{ij} \leq 0$ for all $j \in \{1, \dots, d\}$.

The i -th row of the matrix B describes the mass in pool i : b_{ij} is the rate at which mass moves from pool j to pool i , and b_{ii} is the rate at which mass leaves the pool i which includes transfer to other pools and losses from the system. The rate at which mass enters from outside the system to pool i is given by s_i .

A (linear) *autonomous compartmental system* with d pools is given by an inhomogeneous linear differential equation

$$\dot{x} = Bx + s, \quad (2)$$

where $B \in \mathbb{R}^{d \times d}$ is an invertible matrix, $0 \neq s \in [0, \infty)^d$, and the entries $\{b_{ij}\}_{i,j \in \{1, \dots, d\}}$ of the matrix B satisfy

- $b_{ii} < 0$ for all $i \in \{1, \dots, d\}$,
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4.1 Nonautonomous compartmental system

Let $I := (\tau, \infty)$ with $\tau \in \{-\infty\} \cup \mathbb{R}$ be a time interval, $B : I \rightarrow \mathbb{R}^{d \times d}$ be a bounded continuous function of invertible matrices and $s : I \rightarrow [0, \infty)^d$ be a bounded continuous function. A (linear) *nonautonomous compartmental system* with d pools is given by an inhomogeneous linear nonautonomous differential equation

$$\dot{x} = B(t)x + s(t), \quad (3)$$

where we assume that the entries $\{b_{ij}(t)\}_{i,j \in \{1, \dots, d\}}$ of the matrix $B(t)$ satisfy

- $b_{ii}(t) < 0$ for all $i \in \{1, \dots, d\}$ and $t \in I$,
- $b_{ij}(t) \geq 0$ for all $i \neq j \in \{1, \dots, d\}$ and $t \in I$,
- $\sum_{i=1}^d b_{ij}(t) \leq 0$ for all $j \in \{1, \dots, d\}$ and $t \in I$.

4.2 Mean age system

Consider the nonautonomous compartmental system (3) with a fixed solution $t \mapsto (x_1(t), \dots, x_d(t))$ of positive entries. Let $p_i(a, t)$ be the density function on age a for the mass in pool i at time t (note that $\int_0^\infty p_i(a, t) da = x_i(t)$), and

define the *mean age* of mass in pool i by

$$\bar{a}_i(t) = \frac{\int_0^\infty a p_i(a, t) da}{\int_0^\infty p_i(a, t) da} \quad \text{for all } i \in \{1, \dots, d\}.$$

Then the mean ages $\bar{a}(t) = (\bar{a}_1(t), \dots, \bar{a}_d(t))$ solve the ordinary differential equation

$$\dot{\bar{a}} = g(t, x, \bar{a}), \quad (4)$$

with

$$g_i(t, x, \bar{a}) = 1 + \frac{\sum_{j=1}^d (\bar{a}_j - \bar{a}_i) b_{ij}(t) x_j(t) - \bar{a}_i s_i(t)}{x_i(t)} \quad \text{for all } i \in \{1, \dots, d\}.$$

Combining the equations (3) and (4) yields

$$\begin{pmatrix} \dot{x} \\ \dot{\bar{a}} \end{pmatrix} = \begin{pmatrix} B(t)x + s(t) \\ g(t, x, \bar{a}) \end{pmatrix}, \quad (5)$$

4.3 Nonautonomous residence times

We define residence time as the mean age of mass leaving the system at a particular time t . Note that in our nonautonomous context, this quantity depends on the actual time t . We also provide a formula that corresponds to the mean age of mass currently available in the compartmental system.

4.3.1 Nonautonomous residence time and mean age

Consider the skew product system (5) consisting of the nonautonomous compartmental system (3) and the mean age system (4). The *residence time* of a solution $(x_1(t), \dots, x_d(t), \bar{a}_1(t), \dots, \bar{a}_d(t))$, $t \in I$, of this system is then defined as

$$R(t) := \frac{\sum_{i=1}^d \bar{a}_i(t) x_i(t) \sum_{j=1}^d b_{ji}(t)}{\sum_{i=1}^d x_i(t) \sum_{j=1}^d b_{ji}(t)} \quad \text{for all } t \in I,$$

and then *mean age* of this solution is defined by

$$M(t) := \frac{\sum_{i=1}^d \bar{a}_i(t) x_i(t)}{\sum_{i=1}^d x_i(t)} \quad \text{for all } t \in I.$$

The residence time $R(t)$ is the mean age of a particle (e.g., carbon) leaving the system at time t , where as the mean age $M(t)$ is the mean age of a particle in the system at time t .

By providing measures of mean age and residence time for the nonautonomous case (which agree with definitions for the autonomous case) we provide the first step towards an analysis of temporally varying systems.

5 Temporal autocorrelation

Another approach to thinking about the importance of transients is to recognize the importance of serial autocorrelation in time of forcing terms over realistic ecological time scales. In work with Kim Cuddington, we have analyzed simple models with serial autocorrelation to look at the idea that systems may have a higher likelihood of passing a threshold because of the correlation. These ideas are applied to understanding potential damage from invasive species. Environmental parameters such as temperature and rainfall have a positively autocorrelated variance structure which makes it likely that runs of good or bad conditions will occur. It has previously been demonstrated that such autocorrelated environmental variance can increase the probability of extinction in small populations, in much the same way that increased variance without autocorrelation can increase extinction risk. As a result, it has also been suggested that positive autocorrelation will decrease the probability that a species will establish in a novel location. We suggest that describing the probability of invasion success as the probability of indefinite persistence may be an inappropriate definition of risk.

Economic or ecological damage may be associated with a population that initially reaches high densities before going extinct. In addition, such populations may spread to new locations before extinction. We use a modeling approach to examine the effect of positively autocorrelated conditions on the probability that small populations will reach large size before extinction. We find that where variance is high and the geometric mean of the population growth rate is low, autocorrelation increases the risk that a population will pass a an upper threshold density, even when extinction probability is unaffected. Therefore species classified as having low probability invasion risk on the basis of population growth rates measured in low variance environments may actually have quite a substantial probability of establishing a large population for a period of time. The mechanism behind the effect is the disproportionate influence of short runs of good conditions initially following introduction.

6 Age structure and response to pulses

In earlier work I had used primarily numerical approaches to investigate a problem looking at the role of different time scales of variability on the dynamics of stage structured models. This analysis was restricted to two stage classes and depended on a numerical approach to one part of the problem. The question reduces to the comparison of the spectral bound of a convex combination of matrices with the convex combination of the spectral bounds of the individual matrices. In a collaboration with Professor Pauline van den Driessche of the University of Victoria, we have been able to find analytic approaches to extend the results to arbitrary numbers of classes using methods based on the theory of M-matrices, which is essentially a generalization of Peron-Frobenius theory. These results provide insight into the time scales of response of the systems

studied to external forcing on different scales.

In the continuous time density independent population dynamic model, let y_1 denote the population numbers in the first stage class into which all individuals are born with the numbers in subsequent stage classes denoted by y_i with i ranging from 2 to n . Then the population numbers are described by the vector

$$Y = (y_1, \dots, y_n)^T. \quad (6)$$

Assume that in the good environment, the per capita mortality rate of an individual in stage i is given by μ_i , the rate of maturation from stage i to $i + 1$ is given by γ_i , and the per capita fecundity (rate of production of new individuals) of an individual in stage i is m_i with $\mu_i, m_i > 0$ for $i = 1, \dots, n$, and $\gamma_i > 0$ for $i = 1, \dots, n - 1$. In the bad environment, the parameters are the same except that there is no reproduction, so all $m_i = 0$.

The population dynamics can be described using two real matrices A and B as follows. The $n \times n$ matrix A is defined as

$$A = \begin{bmatrix} -\mu_1 - \gamma_1 + m_1 & m_2 & \cdots & \cdots & m_{n-1} & m_n \\ \gamma_1 & -\mu_2 - \gamma_2 & 0 & \cdots & 0 & 0 \\ 0 & \gamma_2 & \ddots & & \vdots & \vdots \\ \vdots & 0 & \ddots & \ddots & 0 & \vdots \\ \vdots & \vdots & & \ddots & -\mu_{n-1} - \gamma_{n-1} & 0 \\ 0 & 0 & & & \gamma_{n-1} & -\mu_n \end{bmatrix}.$$

Let $B = A - M$, where

$$M = (1, 0, \dots, 0)^T (m_1, \dots, m_n). \quad (7)$$

The model assumes that the environment varies in time, with the dynamics in the good environment given by,

$$dY/dt = AY$$

and in the bad environment by,

$$dY/dt = BY.$$

The ultimate population growth rate in the model depends on the rate of switching between good and bad environments and the fraction of time the environment is good or bad. For a square matrix, $s(X)$, called the spectral abscissa of X (sometimes called the spectral bound of X), denotes the maximum real part of an eigenvalue of X . Let θ be the fraction of time that the environment is in the good state. Assuming that the environment varies arbitrarily rapidly, the long-term population growth rate is given by $\theta s(A) + (1 - \theta)s(B)$ since for sufficiently rapid variation the growth is simply determined by the average environment. If the environment varies on a very slow time scale the long-term

population growth rate is the average of the growth rates in each environment, so is given by $s(\theta A + (1 - \theta)B)$. This latter conclusion depends on the environment remaining in the good or bad state long enough so that the spectral abscissa provides a good description of the growth during that period. The interesting biological question is to determine conditions under which the population grows faster with slow or rapid environmental variation. These conditions depend on the life history, and the stage dependent variation in birth and death rates.

Thus we are interested in comparing the following two quantities

$$SVs = s(\theta A + (1 - \theta)B) \quad \text{and} \quad RVs = \theta s(A) + (1 - \theta)s(B) \quad (8)$$

for $\theta \in [0, 1]$, i.e., comparing the spectral abscissa of a convex combination of A and B with the convex combination of their individual spectral bounds. Since A, B and $\theta A + (1 - \theta)B$ are essentially nonnegative (i.e., all off-diagonal entries are nonnegative, sometimes called quasi-positive), the spectral abscissa of each matrix is also an eigenvalue. Note that if $\theta = 0$ or 1 , then $SVs = RVs$, so from now on it is convenient to take $\theta \in (0, 1]$, then $\alpha = 1/\theta \geq 1$. The behavior for several special cases are clearly suggested by the underlying biological model, so results are given here for more complex cases..

6.1 Equal fecundity and death rates in each stage class

Here, assume $m_i = m$ and $\mu_i = \mu$ for $i = 1, \dots, n$. Then $A = -\mu I + M + G$, where

$$G = \begin{bmatrix} -\gamma_1 & 0 & \cdots & \cdots & 0 \\ \gamma_1 & -\gamma_2 & 0 & \cdots & \vdots \\ 0 & \gamma_2 & \ddots & \ddots & \vdots \\ \vdots & \ddots & \ddots & -\gamma_{n-1} & \vdots \\ 0 & \cdots & 0 & \gamma_{n-1} & 0 \end{bmatrix}. \quad (9)$$

Thus

$$\begin{aligned} SVs &= s(\theta A + (1 - \theta)B) \\ &= s(-\mu I + G + \theta M) \\ &= -\mu + s(G + \theta M) \end{aligned}$$

and

$$\begin{aligned} RVs &= \theta s(A) + (1 - \theta)s(B) \\ &= \theta s(-\mu I + M + G) + (1 - \theta)s(-\mu I + G) \\ &= -\mu + \theta s(G + M) + (1 - \theta)s(G) \\ &= -\mu + \theta s(G + M), \end{aligned}$$

since $s(G) = 0$. Therefore, an equivalent problem is to compare

$$SVs = s(G + \theta M) \quad \text{and} \quad RVs = \theta s(G + M) \quad (10)$$

for $\theta \in (0, 1)$.

If $\rho(F_{X(\alpha)}V_{X(\alpha)}^{-1})$ does not increase for all $\alpha \geq 1$, then $s(X(\alpha)) \leq s(Y)$.

6.2 Equal death rates, monotonic fecundity rates

Let $\alpha = 1/\theta$. Then for $\mu_i = \mu$, the problem is equivalent to comparing

$$SVs = s(\alpha G + M) \quad \text{and} \quad RVs = s(G + M) \quad (11)$$

for $\alpha \geq 1$ with M as in (7) and G as in (9). Setting $X(\alpha) = \alpha G + M$ gives $SVs = s(X(\alpha))$ and $RVs = s(X(1)) = s(Y)$. As in Theorem ??, let $X(\alpha) - s(Y)I = F_{X(\alpha)} - V_{X(\alpha)}$ with $F_{X(\alpha)} = M$ (independent of α) and $V_{X(\alpha)} = s(Y)I - \alpha G$. By noting that M is a nonnegative matrix of rank 1 and $V_{X(\alpha)}$ is a nonsingular \mathcal{M} -matrix with G lower triangular, $\rho(F_{X(\alpha)}V_{X(\alpha)}^{-1})$ can be explicitly calculated; see, for example, [?, p. 707]

$$\rho(F_{X(\alpha)}V_{X(\alpha)}^{-1}) = \sum_{i=1}^n \left(\prod_{k=1}^{i-1} \frac{\alpha \gamma_k}{d + \alpha \gamma_k} \right) \frac{m_i}{d + \alpha \gamma_i} \quad (12)$$

with $d = s(Y)$, $\gamma_n = 0$ and by convention, $\prod_{i=p}^q = 1$ if $p > q$.

6.3 Equal fecundity rates, lowest death rate in the last stage class

Now, assume $m_i = m$ and $\min\{\mu_i\} = \mu_n > 0$ for $i = 1, \dots, n$. From the case with $n = 2$, $SVs \leq RVs$, but we were able to give a proof of this inequality for general n .

6.4 Implications

From a biological perspective, our results provide interesting examples of how the growth rate of a species depends on the relationship between the time scale of environmental variability and the stage dependent pattern of fecundities and death rates. Given that selection should favor those with higher growth rates, our results predict some of the life history patterns that should be observed for species experiencing different temporal scales of environmental variability. Note as well that this clearly means that persistence may depend on the time scale of variability as the population could grow in one instance and decline in another.

7 Dynamic range sizes for territorial animals

Home range sizes of territorial animals are often observed to vary periodically in response to seasonal changes in foraging opportunities. Here we develop the first mechanistic model focused on the temporal dynamics of home range expansion and contraction in territorial animals. We demonstrate how simple movement principles can lead to a rich suite of range size dynamics, by

balancing foraging activity with defensive requirement and incorporating optimal behavior rules into mechanistic home range analysis. Our heuristic model predicts three general temporal patterns that have been observed in empirical studies across multiple taxa. First, a positive correlation between age and territory quality promotes shrinking home ranges over an individual's lifetime, with maximal range size variability shortly before the adult stage. Second, poor sensory information, low population density, and large resource heterogeneity may all independently facilitate range size instability. Finally, aggregation behavior towards forage-rich areas helps produce divergent home range responses between individuals from different age classes. This model has broad applications for addressing important aspects of animal space, with potential applications also in conservation and health.

8 Seasonality

A graduate student who will be supported on the grant during the next year, Easton White, and I have been investigating simple models that incorporate seasonality in a variety of ways, which essentially synthesizes and incorporates many of the ideas just described.

9 Time scales overview

Much of the overall progress from the proposal was summarized in a paper published in PNAS in 2016. Human management of ecological systems, including issues like fisheries, invasive species and restoration as well as others often must be undertaken with limited information. This means that developing general principles and heuristic approaches is important. The importance of an explicit consideration of time arises because of the inherent limitations in the response of ecological systems. Even for linear systems, it is important to recognize the necessary delays in the response of the ecological system to management. General results emerge for optimization approaches to management which emphasize how delays due to demography and life histories can change the optimal management approach. Similar themes emerge in systems with density dependence and tipping points, namely that when considering issues of restoration or management to change the state of an ecological system, that time scales need explicit consideration and may change the optimal approach in important ways.

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